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METABOLIC AND ENDOCRINOLOGICAL CONSEQUENCES OF NUTRITIONAL STRESS IMPOSED OVER SUCCESSIVE LACTATIONS IN PRIMIPAROUS AND MULTIPAROUS SOWS

by

© ELIZABETH SARAH LYTHGOE

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled METABOLIC AND ENDOCRINOLOGICAL CONSEQUENCES OF NUTRITIONAL STRESS IMPOSED OVER SUCCESSIVE LACTATIONS IN PRIMIPAROUS AND MULTIPAROUS SOWS submitted by ELIZABETH SARAH LYTHGOE in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY in ANIMAL NUTRITION.

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ABSTRACT

Forty-nine primiparous and 47 multiparous cross-bred sows were randomly assigned to groups that were fed to appetite (high) or fed at a restricted (low) level during lactation. Twenty-two high-fed, and 21 restricted-fed sows were on trial for two consecutive parities (periods 1 and 2), and of these, 10 high and 12 restricted remained on test for a third parity (period 3). During gestation the sows were housed in individual stalls within close proximity to a boar and fed 2.25 $kg.d^{-1}$ of a 16% crude protein diet which supplied 13.5 MJ kg^{-1} of digestible energy. During lactation the sows were fed a 16% crude protein diet to a scale which allowed 10 (week 1), 13 (week 2) and 14 (weeks 3 and 4) percent of metabolic body weight ($kg^{0.75}$) for sows fed to appetite or 5 (week 1), 6.5 (week 2) and 7 (weeks 3 and 4) percent of metabolic body weight for restricted-fed sows.

The diet for restricted-fed sows was formulated with increased levels of vitamin-mineral premix so that only protein and energy intake of those sows was restricted.

Litter size was standardized to 8 pigs by day 3 of lactation and the pigs did not have access to creep feed. Pigs were weighed at birth and at weekly intervals throughout lactation. Sows were weighed at breeding, day 109 of gestation, and on day 1, 14, and 28 of lactation. On days 2 and 28 of lactation (period 1) the following samples were collected; subcutaneous backfat (9-high, 12-low), milk (12-high, 12-low), and hourly blood samples (12-high, 11-low). Backfat depth was measured ultrasonically on day 2 and 28 of lactation. Two 3-day nitrogen balance trials were conducted with four high and five low fed sows from days 2 and 4 and days 25 and 27 of lactation.

Restricted-fed sows lost more weight ($P<0.001$) and backfat ($P<0.001$), had lower milk yield ($P<0.01$) and weaned fewer and lighter pigs ($P<0.05$, period 3) than sows fed-to-appetite. There were no significant differences in gross milk composition but fatty acid composition of both milk fat and backfat was affected by feeding level ($P<0.01$). Fed-to-appetite sows had greater daily nitrogen retention ($P<0.01$), and lower plasma creatinine concentration ($P<0.01$). Plasma levels of cortisol ($P<0.05$) and growth hormone ($P<0.01$) were higher, while plasma insulin ($P<0.01$) was lower in restricted-fed sows on

day 28 of lactation. Restricted feeding had no effect on ovulation rate, embryo number, or embryo survival, but resulted in a greater incidence of anestrus, and extended weaning to remating intervals in period 3.

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Table of Contents

Chapter	Page
I. INTRODUCTION	1
A. PUBERTY	2
Energy Intake	2
Age at Puberty	2
Ovulation Rate	3
Embryo Survival	3
B. PREGNANCY	3
Energy Intake	4
Body Composition	4
Litter Characteristics	4
Added Fat	5
Protein Intake	5
C. LACTATION	6
Energy Intake	6
Milk Yield and Composition and Litter Performance	6
Sow Weight Change	7
Weaning to Mating Interval	8
Ovulation Rate	8
Energy Requirements for Lactation	9
Protein Intake	9
Body Composition	10
Weaning to Remating Interval	10
D. HORMONE PROFILES DURING POST WEANING ANESTRUS	11
Reproductive Hormones	11
Metabolic Hormones	12
E. CONCLUSION	13

F. REFERENCES 15

II. BODY-WEIGHT, PLASMA CONSTITUENTS, AND ENERGY AND NITROGEN METABOLISM IN RESPONSE TO FEED INTAKE 21

A. INTRODUCTION 21

B. MATERIALS AND METHODS 22

Experimental Design 22

Laboratory Analyses 24

Statistical Analyses 24

C. RESULTS AND DISCUSSION 25

Liveweight and Backfat Changes 25

Plasma Constituents 26

Energy and Nitrogen Metabolism 27

D. REFERENCES 36

III. MILK YIELD AND COMPOSITION, AND SOW REPRODUCTIVE PERFORMANCE 40

A. INTRODUCTION 40

B. MATERIALS AND METHODS 40

Experimental Design 40

Laboratory Analyses 42

Statistical Analyses 43

C. RESULTS AND DISCUSSION 43

Milk Yield 43

Milk Composition 45

Fatty Acid Composition 45

Sow and Litter Performance 46

D. REFERENCES 56

IV. PLASMA PROFILES OF CORTISOL, PROLACTIN, GROWTH HORMONE AND INSULIN ON DAYS 2 AND 28 OF LACTATION 60

A. INTRODUCTION 60

B. MATERIALS AND METHODS 60
Experimental Design 60
Hormone Assays 61
Statistical Analyses 63
C. RESULTS AND DISCUSSION 63
D. REFERENCES 71
V. GENERAL DISCUSSION 74
A. REFERENCES 77

List of Tables

Table		Page
II.1	Formulation and composition of the diet.	29
II.2	Average daily feed intake (kg) during lactation of fed-to-appetite (high) and restricted-fed (low) sows.	30
II.3	Effects of energy and protein restriction during lactation on sow liveweight change (kg) over three successive parities.	31
II.4	Effects of energy and protein restriction during lactation on sow backfat thickness (mm) for period 1.	32
II.5	Effect of feed intake during lactation on plasma levels of free fatty acids, urea nitrogen, glucose and creatinine for period 1.	33
II.6	Effect of feed intake during lactation on energy and nitrogen balance of sows for period 1.	34
III.1	Formulation and composition of the diet.	49
III.2	Effect of energy and protein restriction during lactation on milk production ($kg.d^{-1}$).	50
III.3	Milk composition as percentage in fresh milk from sows fed-to-appetite vs. restricted-fed sows during lactation for period 1.	51
III.4	Effect of protein and energy restriction during lactation (day 28) on fatty acid composition of sow's milk fat.	52
III.5	Effect of protein and energy restriction during lactation on the fatty acid composition of sow subcutaneous adipose tissue.	53
III.6	The effects of energy and protein restriction during lactation on sow performance.	54
III.7	The effects of energy and protein restriction during lactation on litter performance.	55
IV.1	Formulation and composition of the diet.	67
IV.2	Average daily plasma concentrations of cortisol, prolactin, growth hormone and insulin in multiparous sows during lactation.	68
IV.3	Plasma profiles of cortisol and prolactin in multiparous sows fed-to-appetite (high) or restricted-fed (low) during lactation.	69
IV.4	Plasma profiles of growth hormone and insulin in multiparous sows fed-to-appetite (high) or restricted-fed (low) during lactation.	70

List of Figures

Figure		Page
II.1	Flow diagram illustrating the number of sows employed for each of the three lactation periods.	35

I. INTRODUCTION

Nutrition and metabolism have been known to play a vital role in the functioning of the reproductive system for nearly a century. Darwin in 1896 observed that well-nourished animals were more fertile than animals receiving low amounts of feed. Since Darwin's time, much data testifying to the importance of nutritional factors in regulating reproductive function in almost all mammalian species has been collected. Despite the scores of research articles associating body weight and body fat with activity of the reproductive axis no mechanisms by which the body "knows" its metabolic status, or level of body reserves have been explained.

In the pig, attempts to shed light on this problem have been made by studying the effects of protein, energy and feed intake during various stages of the reproductive cycle on sow productivity. The magnitude of these effects is difficult to establish from past experiments due to small numbers of animals and insufficient replication. Past work focused on discrete reproductive stages and the sows' specific requirements were assessed by production characteristics. Recommendations were made on the basis of meeting the animals' nutrient needs to achieve a certain level of productivity for that one particular stage of reproduction. There is increasing evidence to show that reproductive stages are not discrete and that nutrition during a particular stage has both direct and indirect effects on sow productivity. Elsley (1973) and Aherne and Kirkwood (1985) have expressed similar concerns about past experiments.

Past feeding recommendations are insufficient to meet current expectations of continued productivity. This problem may be due in part to vigorous breeding programs which have resulted in gilts being progressively younger and leaner when they enter their reproductive life (Whittemore and Pearce, 1980). Consequently, today's sows have fewer body reserves from which to draw and are therefore, more suceptible to nutritional inadequacy.

A. PUBERTY

Gilts comprise 30-40% of the breeding females of a herd (Aherne and Kirkwood, 1985) and therefore, their contribution to herd productivity is significant. Body composition of the gilt has a major influence on longevity and reproductive performance. Brooks (1982) suggested that the level of reserves (evaluated by live weight and ultrasonic measurements of backfat thickness) may be used as an indicator of successful reproductive performance. Maximum productivity of gilts is determined by age at mating, ovulation rate, litter size, and ability to be successfully remated.

Energy Intake

Age at Puberty

Early onset of puberty is important in attaining maximum productivity in terms of the number of pigs produced and there is considerable literature on the effects of nutrition on age and weight at puberty. It is generally accepted that severe energy restriction (50% of ad libitum) will retard somatic growth, and since reproductive development has low priority for dietary energy, the onset of puberty will be delayed (Aherne and Kirkwood, 1985).

Less severe energy restriction (60 to 70% of ad libitum) has given variable results. A review of the literature by Anderson and Melampy (1972) showed that in 9 experiments restricted energy intake delayed puberty by an average of 16 days, while puberty onset was hastened by an average of 11 days in 5 others. Etienne et al. (1983) reported that large differences in the age at puberty resulted when energy was restricted to 33% of ad libitum during the growing period. It has been suggested that there is a critical period during growth when a moderately severe restriction will retard development but once beyond this period only a very severe (50% or greater) restriction will delay puberty (Aherne and Kirkwood, 1985). Aherne and Kirkwood (1985) reported that there is a general agreement the literature that moderate restriction during the rearing period will not influence puberty attainment.

Ovulation Rate

Once puberty has been reached nutrition, during the estrus cycle has a significant effect on ovulation rate. Several authors have shown that increased feed or energy intake 11 to 14 days before mating results in a greater number of ova shed (Brooks and Cole, 1984; Den Hartog and van Kempen, 1980; King and Williams, 1984c). Flushing appears to have beneficial effects primarily in undernourished animals (Brooks and Cole, 1974). The mechanism by which flushing exerts its' influence is not known and it may be that flushing only increases the ovulation rate to that which would normally be expected with proper feeding.

Embryo Survival

Analysis of a large number of trials by Den Hartog and van Kempen (1980) showed that high level feeding during rearing (19 trials) or in the premating period (36 trials) is associated with increased embryonic mortality. The reasons for this are unclear, but it has been suggested that gilts having high energy intakes have increased ovulation rates and this in turn leads to increased embryonic mortality (Anderson and Melampy, 1972; Den Hartog and van Kempen, 1980; Aherne and Kirkwood, 1985). Other researchers have not found this effect (Heap et al., 1967; Pike and Boaz, 1972; Dyck, 1974; Toplis et al., 1983). The detrimental effect is not seen in trials where older animals are used (Toplis et al., 1983; Aherne and Kirkwood, 1985). There is some evidence to support the hypothesis that the effect is mediated by a decrease in plasma progesterone which has been associated with increased feed or protein intakes during early pregnancy (Jordan and Swanson, 1979; Dyck et al., 1980; Aherne and Kirkwood, 1985).

B. PREGNANCY

During pregnancy the sow requires nutrients to meet the demands of the developing conceptus and to achieve some weight gain in the maternal tissue. Early in development (first two months) the conceptus has little demand for nutrients consequently most of the retained

nutrients are deposited in the maternal body. Later, development is characterized by acceleration in conceptus growth which changes both the priority and demand for nutrients. On a restricted feeding level, the increase in requirement for conceptus gain is achieved by catabolism of maternal body reserves (O'Grady, 1980; Close and Cole, 1986; Close, 1987).

Energy Intake

Body Composition

The level of feeding influences the rate and extent of tissue accretion in the maternal body and consequently in the body weight gain of the sow (Close and Cole, 1986). During pregnancy there are major changes in the rate of protein and fat deposition. Close et al. (1985) examined the heat losses and energy and nitrogen balances of pregnant gilts at feed intakes of 1.8 or 2.5 kg.d^{-1} (20 and 30 MJ metabolizable energy (ME), respectively) at an environmental temperature of 20°C. Maximum protein deposition occurred from day 70 of pregnancy to parturition and was relatively independent of level of feeding. Most of the deposition was associated with the accretion in reproductive tissue. Fat deposition depended on level of feeding and it was calculated that by day 110 of gestation, gilts on the lower intake were mobilizing 140 g fat.d^{-1} from maternal stores. Gilts given 2.5 kg feed.d^{-1} remained in positive energy and fat balance throughout pregnancy. It is apparent that loss of body tissue following repeated and prolonged application of low feed levels would result in severely emaciated sows with a high incidence of infertility.

Litter Characteristics

According to a literature review of Elsley (1973), feed intake in pregnancy is highly correlated with live weight gain of sows ($r=0.71$), moderately correlated with piglet birth weight ($r=0.46$) and poorly correlated with litter size ($r=0.14$). Other workers have reported that increasing pregnancy feed or energy intakes up to 2.2 kg feed.d^{-1} (25 MJ ME.d^{-1}) resulted in a progressive increase in piglet birth weight (Libal and Wahlstrom, 1977; ARC,

1981; Close et al., 1984). Some researchers have suggested that the pattern of feed intake throughout pregnancy should not be constant but rather should parallel foetal development. Most studies indicate that the total amount of feed given is more important than the pattern of intake (Aherne and Kirkwood, 1985). In one study by Elsley et al. (1971), sows at several research centres were given a total of 220 kg of feed during pregnancy with varying patterns of intake. There was no significant effect on the number of piglets born, their average birth weight, or breeding regularity of the sows over 3 parities.

Added Fat

Experiments aimed at increasing the energy reserves of piglets and thus their survival at birth have been approached by manipulation of the sows' nutrition during late pregnancy. Seerley et al. (1974; 1978) found that the addition of lipids to the dams' diet prior to parturition did not significantly affect the number or weight of piglets born. Body energy reserves of the piglets, and the fat content of colostrum and milk were slightly increased. It is generally concluded that the effects of added fat to the sows' diet is dependent upon the condition of the sow and thus her ability to provide nutrients for growth and development (Close and Cole, 1986).

Protein Intake

Variations in protein intake during pregnancy do not appear to influence litter size at birth but do affect birth weight (O'Grady, 1980; Shields et al., 1985; Close and Cole, 1986). Sow weight gain during gestation is increased by feeding higher levels of protein with maximum gain being achieved with 300 g crude protein.d^{-1} (O'Grady, 1980; Aherne and Kirkwood, 1985). Reproductive performance is maximized when the sow is given 140 to 180 g crude protein.d^{-1} supplying 8-10 g of lysine, 7-8 g threonine and 1.5 g tryptophan (O'Grady, 1980). Until recently the effects of gestation protein intake on sow performance and body composition had not been examined. An experiment by Shields et al. (1985) in which sows were given 1.82 kg.d^{-1} of either a 5 or 14% protein gestation diet resulted in differences in

maternal tissue accretion and litter characteristics. Sows fed the 5% protein gestation diet had more maternal fat but less protein accretion than those fed the 14% protein gestation diet. During the last trimester of pregnancy the sows fed the 5% protein diet mobilized body protein reserves probably to support the growth of conceptus products. Mobilization of body tissue reserves resulted in the sows having a lower maternal body weight gain relative to the sows fed the 14% protein diet (10 and 26 kg gain, respectively). Pig birth weight was reduced and postpartum mortality was higher for sows fed the 5% protein diet. Sows given the 14% protein diet had lower maternal fat accretion and higher individual pig birth weights implying that there was a greater diversion of dietary energy toward conceptus product formation.

C. LACTATION

The sow has the capability of producing copious quantities of milk to meet the needs of her suckling litter. The most important factors influencing milk production are the nutritional state of the sow and her protein and energy intake, and the demands made by the litter (Close and Cole, 1986; Close, 1987). It has been suggested by O'Grady et al. (1985) that sows are normally given insufficient feed to meet the requirements for maintenance and milk production. The factors that limit feed intake are management and husbandry practices which restrict the amount given to sows, and the sows' appetite capacity (O'Grady et al., 1985; Close and Cole, 1986). The end result is a decrease in milk yield and/or excessive body weight loss which may adversely affect subsequent reproductive performance.

Energy Intake

Milk Yield and Composition and Litter Performance

Conclusions made on the basis of short term experimentation may differ significantly from those drawn from studies conducted over several parities. This is demonstrated by the work of O'Grady et al. (1973) in which lactating gilts were given varying energy intakes (51 to 86 MJ DE.d^{-1}) for three consecutive lactations. The results indicated that energy intake

during the first lactation had no effect on milk yield, milk composition or litter growth. Other authors have reported similar findings (Libal and Wahlstrom, 1977; ARC, 1981; O'Grady et al., 1985). During the second lactation milk yield of the sows on the lower energy intake was impaired, and by the third lactation both milk yield and piglet growth were markedly depressed.

Energy intake during lactation has been shown to influence the fat content of milk and piglet body composition. Noblet and Etienne (1986) fed lactating sows 3.5 or 5.0 kg of feed.d^{-1} (44 and 59 MJ ME.d^{-1} respectively). Sows on the lower energy intake had lower milk yield but the milk was higher in fat. Energy intake had no effect on litter growth rate, but piglets from sows on the low energy intake had greater dry matter, fat and energy content in their bodies at weaning. The data suggests that the sows receiving 3.5 kg of feed.d^{-1} mobilized body lipids in order to maintain energy output in milk. If the experiment had been continued over successive parities it is probable that the sows' ability to maintain energy output and piglet growth would decrease as body reserves were depleted.

The ARC (1981) concluded that energy intake during lactation has little effect on piglet growth but the demands of lactation are significant and if not met by the diet they are supplied from mobilization of maternal body reserves.

Sow Weight Change

Many researchers have shown that weight change of sows during lactation responds to energy intake (Hitchcock et al., 1971; O'Grady et al., 1975; ARC, 1981; Aherne and Kirkwood, 1985). It has been suggested by O'Grady et al. (1985) that lactating sows need to consume 76.8 MJ ME.d^{-1} in order to maintain body weight. This level is likely to be beyond the animals appetite capacity and as a result most lactating sows experience loss of weight and mobilization of fat reserves (Reese et al., 1982a,b; King and Dunkin, 1986b; Noblet and Etienne, 1986) and muscle tissue (Reese et al., 1982a; Etienne et al., 1985) in order to maintain milk production.

Weaning to Mating Interval

Nutrition during lactation influences weight and body condition of sows at weaning, and thus affects sow productivity (Aherne and Kirkwood, 1985). Recent studies report that excess loss of live weight or body condition results in extended weaning to remating intervals, and an increased incidence of anestrus (King et al., 1982; 1984; Reese et al., 1982a,b; King and Williams, 1984a,b; King and Dunkin, 1986a,b). The critical level of body weight or condition below which reproductive performance is impaired or the minimum level of dietary energy intake required to prevent this is unknown (Aherne and Kirkwood, 1985). Prolonged weaning to mating intervals are associated with lactation energy intakes of 32.2 MJ ME.d^{-1} or less (Reese et al., 1982a,b; 1984; King and Williams, 1984a,b). Increasing energy intake up to 48.0 MJ ME.d^{-1} shortened the remating interval but there was no improvement beyond this level (Reese et al., 1982a).

The time taken to achieve estrus appears to be influenced more by backfat loss than by weight change per se (Reese et al., 1984). Sows given a low energy intake during lactation were divided into groups based on the occurrence of estrus. In both groups lactation weight loss was similar but those that failed to return to estrus had a lower calculated percentage body fat. It is interesting to note that the data collected by Esbenshade et al. (1986) did not reveal significant relationships between changes in body condition and rebreeding performance of sows. These authors monitored a commercial farrow to finish unit over a one year period. Body condition was evaluated by change in body weight, heart girth, backfat thickness and condition score. During lactation the sows were fed ad libitum, and it may be that the changes in body condition were too subtle to have an affect on reproductive performance.

Ovulation Rate

The general conclusion in the literature is that ovulation rate is not influenced by feed intake during lactation (Aherne and Kirkwood, 1985). The work of King and Dunkin (1986a,b) supports this conclusion. In one of their studies, (King and Dunkin, 1986a) sows were given various levels of feed during lactation (1.5 to 4.8 kg.d^{-1}) and although sow live

weight responded to feed intake, there was no effect on ovulation rate. Similar results were found in another of their experiments in which lactating sows were given various combinations of energy and protein levels (King and Dunkin, 1986b). The weaning to mating interval, and the proportion of sows exhibiting estrus within eight days of weaning were improved by higher lactation levels of energy and protein intake.

Energy Requirements for Lactation

Energy for milk production is derived from body tissue and from energy in the feed. The energetic efficiency of milk production is determined by the ratio of these energy sources and the energy content of the milk (De Lange et al., 1980; Verstegen et al., 1985). Literature values on the energetic efficiency of milk production from feed vary depending on the method of calculation and the way in which milk production and metabolic rate of piglets were detemined.

The work of Verstegen et al. (1985) estimated the efficiency of milk production from feed to be 67 to 69% with a maintenance requirement of 112 to 125 kcal ME $W^{.75}.d^{-1}$. From this it was calculated that a sow needs to receive 0.5 to 0.6 kg of extra feed (1500 to 1800 kcal ME) per day for each piglet in order to support milk production. This required amount is greater than the rule of thumb of 0.25 kg of extra feed (750 kcal ME) per day per piglet. The lower amount of feed per piglet would result in maternal body tissue reserves being catabolized in order to meet the energy demands of milk production.

Protein Intake

Recent evidence (Shields et al., 1985) suggests that protein intake during pregnancy and lactation has considerable a primary influence on changes in sow body composition and the occurrence of estrus after weaning.

Body Composition

Shields et al. (1985) demonstrated a clear relationship between gestation protein level and post partum tissue catabolism. Sows given a 5% (low) gestation protein level catabolized small amounts of body protein but experienced a substantially greater loss of maternal fat than sows given a 14% (high) gestation protein diet. The fat balance of the sows on the 14% protein level approached a state of equilibrium. Their results imply that tissue nutrient reserves stored during pregnancy are mobilized upon parturition. The extent of catabolism is dependent upon nutrient status and nutrient demand for initial milk secretion. Sows with greater reserves have greater post partum tissue catabolism, but this may be modified by the diet provided during lactation.

In the same experiment, sows were given 5, 14 or 23% protein levels during lactation. Sows on the 5% protein level lost less live and estimated maternal body weight than the sows on the 14% protein level even though feed consumption was similar. This was explained on the basis of their lower productivity shown by higher piglet mortality, lower litter weight gains, and lower milk production. The authors calculated that during lactation the sows on the low protein level lost approximately 900 $g.d^{-1}$ of maternal body tissue regardless of gestation protein level. The composition of tissue catabolized was influenced by gestation protein level. Sows given low protein levels during both gestation and lactation lost more fat but less protein than sows given higher protein levels in gestation. This implies that sows entering lactation in a protein-depleted condition are unable to deplete body reserves further because nutrient stores have already been used for conceptus development.

Weaning to Remating Interval

Protein and lysine intake during lactation appears to influence the weaning to remating interval. In first-litter sows the incidence of postweaning anestrus is reduced by minimum daily intakes of 56 to 58 MJ ME, 700 to 750 g crude protein and 31 to 37 g lysine (King and Williams, 1984a,b; King and Dunkin, 1986b). Other workers have reported an increase in the percentage of first-litter sows exhibiting estrus within 7 days of weaning when

protein intake during lactation was increased from about 400 g to 725 $g.d^{-1}$ (O'Grady and Hanrahan, 1975; Brendemuhl et al., 1984). In contrast to the effect of protein and lysine intakes during lactation, increasing daily energy intake above a minimum level of 48 MJ $ME.d^{-1}$ does little to improve the weaning-to-estrus interval (Reese et al., 1982; Cox et al., 1983). The mechanism by which protein influences ovarian activity after weaning requires investigation. It is thought that nutrition acts at the level of the hypothalmus and that nutritional deprivation in some unresolved manner reduces gonadotrophin secretion thus inhibiting the occurrence of estrus (Gauthier et al., 1983; Steiner, 1987). Further investigation is needed to elucidate the endocrine control of ovarian activity in the weaned sow and to determine the physiological roles that protein and energy play.

D. HORMONE PROFILES DURING POST WEANING ANESTRUS

Reproductive Hormones

Follicular development during early lactation in the sow is characterized by a large number of small-size follicles and a smaller number of medium-sized follicles (less than 5 mm). The advancement of lactation leads to a gradual increase in the population of medium and large follicles (8 mm or greater) and a decrease in the percentage of atretic follicles (Craighton and Lamming, 1969; Britt et al., 1985). Follicular growth is influenced by gonadotrophin secretion by the anterior pituitary but the exact roles which leutinizing hormone (LH) and follicle-stimulating hormone (FSH) play are not completely known. There is evidence to support the role of FSH in stimulating development of follicles up to the 5-6 mm stage, whilst LH is thought to be involved in the final stages of follicle maturation and ovulation (Elsaesser and Parvizi, 1980; Britt et al., 1985). The positive feedback response of LH to estradiol changes during lactation, is thought to influence follicle maturation and ovulation (Elsaesser and Parvizi, 1980).

Stevenson et al. (1981) showed that during lactation LH secretion is controlled primarily by suckling intensity of the litter, while FSH release is controlled by a non-steroidal

ovarian factor thought to be inhibin. These authors hypothesized that suckling inhibits gonadotrophin releasing hormone (GnRH). Thus at weaning there is an increase in GnRH within the hypothalmus and simultaneously an increase of LH in the anterior pituitary and plasma resulting in follicular growth. It has been suggested by Kirkwood et al. (1984) that sows exhibiting post weaning anestrus are similar to sows weaned at birth (zero-weaned). Sows weaned at birth have a high incidence of cystic follicles and delayed estrus apparently caused by inhibition of the positive feedback response of LH to estradiol (Peters et al., 1969b; Elliot et al., 1980).

Estrus and ovulation can be stimulated in anestrus sows by the administration of GnRH (Kirkwood et al., 1984; Armstrong and Britt, 1985) or estradiol (Dyck et al., 1979; Cox et al., 1983). Success is dependent upon stimulating the follicles sufficiently, so that endogenous secretion of estrogen leads to a positive feedback surge of LH (Britt et al., 1985).

Metabolic Hormones

There is a paucity of information about how hormones, other than the gonadotrophins, affect follicular development and the attainment of ovulatory estrus. Despite the lack of information, it is becoming increasingly evident that metabolic hormones and substrates play a role in linking the body's energy regulating components and the reproductive state of the animal. In monkeys, restricted feeding has been associated with reduced gonadotrophin secretion. Concomitant with this reduction in gonadotrophin secretion is a decrease in plasma insulin and thyroid hormone levels, an increase in levels of plasma cortisol and alterations in circulating amino acid levels (Steiner, 1987).

There is some evidence implicating the role of cortisol in the occurrence of anestrus. The work of Kunavongkrit (1984, cited by Britt et al., 1985) looked at plasma cortisol levels in zero-weaned sows and sows nursing small (2 to 6 pigs) or normal (7 to 9 pigs) litters. Anovulatory zero-weaned sows had elevated plasma levels of cortisol during the first two weeks after parturition relative to those sows that ovulated within two weeks post partum. Cortisol concentrations in sows nursing small and normal size litters were similar to those

observed in the anovulatory zero-weaned sows. It is possible that the elevated cortisol levels block the ability of estradiol to induce the positive feedback surge of LH.

The work of Armstrong et al. (1986) failed to show an effect of restricted feeding on plasma levels of prolactin and insulin in lactating sows. Energy restriction had no effect on reproductive performance or reproductive hormones despite the greater weight and backfat loss of restricted-fed sows relative to sows fed ad libitum. Possibly the effect of energy restriction on hormone concentration was masked by the greater protein intake of the restricted-fed sows compared to that of the sows fed ad libitum (630 vs. 568 $g.d^{-1}$ for restricted-fed and ad libitum, respectively). Another factor that may have influenced the results obtained was the limited blood sampling. Prolactin and insulin concentrations were determined on the basis of a single sample taken on days 6, 12 and 20 of lactation and as a result true differences may have been missed.

For the past two decades, plasma concentrations of hormones have been typically measured by radioimmunoassay methods. Radioimmunoassay techniques utilize antibodies that are specific for the hormone molecule being measured. Thus, these techniques determine the immunoreactivity of the hormone which ideally reflects biological activity of the hormone. Besser et al. (1971) have suggested that plasma hormone concentrations measured by radioimmunoassay in general, accurately reflect the physiological status of the individual. However, it is possible that the absolute values determined by radioimmunoassay may differ in some circumstances, from those determined by bioassay. For this reason, caution should be exercised when equating immunoreactivity with true biological activity.

E. CONCLUSION

The overt effects of environmental and management factors on reproductive performance are well known. The general concensus in the literature is that these factors exert their influence at the level of the ovary and in particular influence follicular development through an effect on gonadotrophin secretion. What is not understood are the factors linking the animals' energy-regulating components with reproductive function, and how these

mechanisms exert their influence on follicular development. A better understanding would enable the development of environmental and management practices that could maximize sow productivity.

The objectives of the studies described herein were to determine the effects of feed restriction during lactation on:

1. body weight change, plasma free fatty acids, glucose, urea nitrogen, creatinine concentrations, and energy and nitrogen metabolism.
2. milk yield and composition, litter growth rate, and sow reproductive performance.
3. twenty-four hour plasma profiles of cortisol, prolactin, growth hormone and insulin on day 2 and 28.

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II. BODY-WEIGHT, PLASMA CONSTITUENTS, AND ENERGY AND NITROGEN METABOLISM IN RESPONSE TO FEED INTAKE

A. INTRODUCTION

Reproductive dysfunction as the result of nutritional stress has been the focus of a large number of recent investigations. The influence of nutritional regimen during lactation on the incidence of postweaning anestrus has been approached from the influence of energy intake (Reese et al., 1982a,b; 1984), protein intake (King and Dunkin, 1986a,b) and total nutrient intake (King et al., 1982; 1984). It is generally concluded that failure to meet the nutrient requirements of gestation and/or lactation results in mobilization of maternal tissue reserves. Excessive depletion of body tissue reserves is associated with loss of reproductive function (Aherne and Kirkwood, 1985). It has been suggested that effects of malnutrition on reproduction are more severe in primiparous than multiparous sows (Reese et al., 1982a,b; Kirkwood and Aherne, 1985).

Documentation demonstrating the inverse relationship between feed intake and weight loss is abundant (Aherne and Kirkwood, 1985). Equally well documented is the existence of a relationship between sow weight change, subcutaneous backfat thickness, and subsequent reproductive performance (Reese et al., 1982a,b; 1984, King and Williams, 1984a, King et al., 1984). The factors responsible and the mechanism by which these factors alter reproductive performance have not been clearly defined.

The experiment herein was designed to study the consequences of chronic energy and protein restriction on (1) body weight change, (2) plasma free fatty acids (FFA), glucose, urea nitrogen (BUN), and creatinine concentrations, and (3) energy and nitrogen metabolism in lactating sows.

B. MATERIALS AND METHODS

Experimental Design

The study was conducted with 49 primiparous and 47 multiparous (2nd to 5th parity) cross-bred sows. The sows were randomly assigned to groups that were fed to appetite (high) or fed at a restricted (low) level during lactation. Twenty-two high-fed, and 21 restricted-fed sows were on trial for two consecutive parities (periods 1 and 2), and of these, 10 high and 12 restricted remained on test for a third parity (period 3). A flow diagram illustrating the number of sows employed for each of the three lactation periods is shown in Figure II.1. Some of the sows were assigned to a second experiment to determine the effects of exogenous gonadotrophin-releasing hormone on sow reproductive performance (Kirkwood et al., 1987) and therefore the number of sows in each period decreased. From weaning to estrus, and during gestation the sows were housed in individual stalls within close proximity to a boar and fed 2.25 $kg.d^{-1}$ of a 16% crude protein diet which supplied 13.5 MJ kg^{-1} of digestible energy. On day 109 of gestation sows were weighed, and moved to raised farrowing crates in the farrowing unit. The temperature of the farrowing unit was maintained at 20°C. During lactation the sows were fed a 16% crude protein diet (Table II.1) to a scale which allowed 10 (week 1), 13 (week 2), and 14 (weeks 3 and 4) percent of metabolic body weight ($kg^{0.07}$) for sows fed to appetite or 5 (week 1), 6.5 (week 2), and 7 (weeks 3 and 4) percent of metabolic body weight for restricted sows.

These lactation feed intake levels were derived in a preliminary study in which 11 multiparous cross-bred sows were fed a similar diet to appetite over a 28 day lactation. Average weekly feed intake was calculated as a percentage of post-farrowing (day 1 of lactation) metabolic body weight.

The diet for restricted-fed sows was formulated with twice the amount of vitamin-mineral premix so that only protein and energy intake of those sows was restricted. Feed regimens were initiated the day after farrowing (day 1), and feed intake was measured daily throughout the 28 day lactation. Litter size was standardized to 8 pigs by day 3 of

lactation and maintained at that number by substitution from litters of the same age whenever necessary. The pigs did not have access to creep-feed. Pigs were weighed at birth and at weekly intervals throughout lactation.

Sows were weighed at breeding, day 109 of gestation, and on day 1, 14, and 28 of lactation. For 54 sows, subcutaneous backfat depth was measured ultrasonically (Kraut Kramer US K7) immediately behind the last rib and 4 cm from the midline on day 2 and 28 of lactation.

Two 3-day nitrogen balance trials were conducted with 4 sows fed to appetite and 5 restricted-fed sows from days 2 to 4, and days 25 to 27 postpartum. Urine was collected through indwelling Foley-cathers (French size 18, 5 mL balloon-type) into glass bottles containing 5 mL 0.3% mercuric chloride in glacial acetic acid (Rocks, 1977). A one percent sample was collected daily, composited for the 3-day collection period and stored at -20°C for later analysis. Total feces were collected daily, placed in plastic bags, weighed, mixed and a 20% sample was frozen. The collections were freeze-dried (Virtis 50-SRC, shelf temperature 22°C for 5 days), ground in a Wiley mill and stored for later analysis. Milk production was estimated using a conversion of 4.0 g of milk per 1.0 g of pig gain (Lucas and Lodge, 1961). Milk ejection was accomplished by intramuscular injection of 1 mL oxytocin (20 USP units per mL, Kovet Ltd.). Milk samples were obtained by hand-milking a thoracic, abdominal, and inguinal pair of teats on the 2nd and 28th day postpartum. The baby pigs were removed from the sow for 50 minutes prior to milk collection.

Blood samples (10 to 15 mL) were collected hourly over a 24-hour period from 12 high-fed and 11 restricted-fed sows on days 2 and 28 of lactation (period 1). The blood samples were obtained from ear vein cannulas (Evans, 1987) and collected into heparinized glass tubes. The samples were placed on ice and centrifuged within 24 hours of collection. Aliquots of plasma were transferred to sterile plastic vials (1.25 x 2.5 cm) and stored at -20°C until required for analysis. Analyses for FFA, glucose, BUN, and creatinine were completed on pooled plasma samples composed of a minimum collection period of 16 hours.

Laboratory Analyses

Feed, fecal, and urine samples were analyzed for dry matter (AOAC, 1980), total Kjeldahl nitrogen (AOAC, 1980), and gross energy of combustion (Harris, 1970). Prior to calorimetry, 100 mL urine samples were freeze-dried and a portion weighed into 10 mL polystyrene disposable cups (Fisherbrand) for combustion. The amino acid composition of the diet was determined on a Beckman 121MB amino acid analyzer after acid (6 N HCl) hydrolysis of the feed protein. Milk was analyzed for protein, fat and lactose using an infra-red auto milk analyzer (Milko Scan 104, Foss Electric). Prior to analysis samples were thawed and homogenized on a polytron (Kinematica GmbH). Dry matter was determined following the AOAC (1980) procedure. The gross energy content of milk in calories per 100 g was calculated using the following formula:

$$E=9.11F + 5.12(6.38 \times TN) + 3.95L$$

where F, TN, and L are percentages of fat, total nitrogen and lactose, respectively. The numerical values, 9.11, 5.12, and 3.95 are combustion factors in calories per gram of fat, protein and lactose, respectively (Perrin, 1954).

Plasma glucose (Trinder, 1969) and FFA (Shimizu et al., 1979) levels were determined enzymatically. The method of Shimizu et al. (1979) was modified by deproteinization prior to the addition of reactants. Blood urea nitrogen analysis was conducted on a Technicon Auto Analyzer following the procedure of Marsh et al., (1965). Plasma creatinine concentration was determined using the colorimetric method of Heinegard and Tiderstrom (1973).

Statistical Analyses

Treatment, parity, and period effects on body-weight change, and subcutaneous backfat depth were tested using MANOVA of SPSSX (SPSS Inc., 1983). All means reported are least-square means. Plasma constituents and energy and nitrogen balance data were tested using a Student's t-test (Steele and Torrie, 1980).

C. RESULTS AND DISCUSSION

Average daily feed intakes for sows and gilts for each week of lactation and for each period are shown in Table II.2 The average feed consumption of all three periods for sows fed to appetite was 4.4, 5.9, 6.2, and 6.3 $kg.d^{-1}$ for weeks one through four of lactation respectively. Daily feed intake during lactation for sows fed the restricted feed level was 54% of that consumed by sows fed to appetite. Feed intake for sows fed to appetite increased greatly from the first to second week of lactation with little further increase thereafter. Sows ate more than gilts in period one (5.5 and 5.1 for high-fed sows and gilts respectively). Feed intake for sows fed to appetite rose with subsequent lactation periods similar to the findings of O'Grady et al. (1985) in which an increase in feed intake was associated with increasing parity. Feeding sows to appetite resulted in no apparent adverse effects in terms of constipation or milk-related problems. Unlike high-fed sows, animals given the restricted feeding level were constantly agitated, and were less willing to allow the baby pigs to nurse. English (1970), and Zoipoulos et al. (1978) also observed that feeding sows to appetite during lactation reduced restlessness and the incidence of injury and baby pig deaths.

Liveweight and Backfat Changes

The average initial body weights were 128 kg (gilts), 161 kg (2nd and 3rd parity sows), and 194 kg (4th and greater parity sows). Sow liveweight changes during the experiment are shown in Table II.3. The weight of the sows at the start of the experiment increased ($P<0.001$) with parity but there were no significant differences in gestation weight gain between sows of similar parity when fed to appetite or restricted-fed during lactation. Previous experiments in which feed intake (Elsley et al., 1969; Hitchcock et al., 1971) or energy intake (Adam and Shearer, 1975; O'Grady et al., 1975) were restricted during lactation had no effect on subsequent gestation weight gain. Despite the lack of statistical significance, restricted feeding for two consecutive lactations resulted in these sows having slightly greater gestation weight gain than sows fed to appetite (41 kg versus 37 kg respectively) in period three. These results support the results of Reese et al. (1982) in which it was observed that

sows given low energy levels during lactation compensated for their greater lactation weight loss by gaining slightly more weight in gestation than sows having high lactation energy intakes.

All sows except the high-fed gilts lost weight during lactation with low-fed sows losing significantly more weight ($P<0.001$) than sows fed to appetite. Restricted feeding resulted in an average lactation weight loss of 26 kg for gilts, and 31 kg for sows. Feeding to appetite resulted in gilts gaining 16 kg, while the sows had an average weight loss of 9 kg over each lactation. Similar weight losses with underfeeding were reported by Elsley et al. (1969), Lodge (1969), Hitchcock et al. (1971) and Libal and Wahlstrom (1977). The interaction of treatment by time was highly significant ($P<0.001$) with weight loss in sows fed to appetite being constant over the lactation while restricted-fed sows lost more weight in early than late lactation (16.5 kg vs 13.0 kg for day 1 to day 14, and day 14 to day 28 of lactation, respectively). From breeding to weaning the high-fed sows gained approximately 27 kg for periods 1 and 2, and 5 kg in the third period. Restricted-fed sows gained only 8 kg in period 1, 2 kg in the second period and lost 8 kg in the final period.

Initial backfat thickness (Table II.4) was greatest ($P<0.05$) for gilts (21.4 mm), and as parity increased backfat thickness decreased (19.1 mm for sows of second or greater parity). Similar results have been reported by Whittemore et al. (1980). Regardless of feeding level all sows mobilized backfat during lactation, the loss being greater ($P<0.001$) for restricted-fed animals (6.4 mm versus 1.3 mm for high-fed sows). Gilts tended to lose slightly more backfat than older sows but the difference was not significant. The interaction of parity by time was highly significant ($P<0.001$) with gilts mobilizing greater amounts of backfat during early lactation while sows experienced their greatest depletion during the latter part of lactation.

Plasma Constituents

The effects of lactation feed intake on plasma levels of FFA's, BUN, glucose and creatinine are shown in Table II.5. There was a trend for plasma FFA concentration to

increase from day 2 to day 28 of lactation (period one) for restricted-fed sows and may be a reflection of increased adipose tissue degradation. In constrast, plasma FFA levels for high-fed sows were constant over the lactation.

There were no significant differences in plasma levels of glucose or blood urea nitrogen, either with treatment or time. Reese et al. (1982a, 1984), reported significantly higher rates of amino acid catabolism as evidenced by increased serum urea nitrogen levels (20.4 versus 10.8 mg dL^{-1}) in sows fed low versus high energy diets during lactation. These levels are considerably lower than those found in the present experiment. Since blood urea nitrogen is the product of protein digestion and tissue-protein metabolism (Blick and Liles, 1985) the high plasma levels observed in sows fed to appetite is most likely the result of ingestion of large amounts of dietary protein. Similiar BUN concentrations were found for restricted-fed sows as for sows fed to appetite. These animals recieved only 50% of the protein allowed to high-fed sows of similiar metabolic body weight, and therefore a greater proportion of the total urea nitrogen must be the product of tissue-protein degradation.

The concentration of plasma creatinine (index of muscle catabolism) supports this conclusion. On day 2 of lactation there were no distinguishable treatment differences in creatinine concentration. By late lactation, creatinine levels had risen significantly ($P<0.01$) in restricted-fed sows while plasma levels in sows fed to appetite declined. Increasing plasma creatinine concentrations are associated with muscle wasting (Wallach, 1978; Blick and Liles, 1985). Catabolism of muscle and adipose tissue apparently occurred in an attempt to meet the requirements of maintenance and lactation in restricted-fed sows. It appears that weight loss in lactating sows results from both catabolism of adipose tissue (Reese et al., 1982a,b; King and Dunkin, 1986; Noblet and Etienne, 1986) and muscle tissue (Reese et al., 1982a; Etienne et al., 1985).

Energy and Nitrogen Metabolism

As was expected, energy ($P<0.05$) and nitrogen ($P<0.01$) intake was greater for both balance periods for sows fed to appetite (Table II.6). In these sows average daily nitrogen

retention was 32 g ($P<0.01$), and 36 g ($P<0.001$) for balance periods 1 and 2, respectively, while that for restricted-fed sows was -5.0 $g.d^{-1}$ and 7.0 $g.d^{-1}$. The increase in nitrogen balance from period 1 to period 2, shown by restricted-fed sows is possibly due to improved utilization of absorbed nitrogen. Fecal nitrogen and energy excretion was greater ($P<0.001$) for high-fed sows and there was a significant increase ($P<0.001$) by balance period 2, presumably due to high feed intake. Urinary energy and nitrogen losses were similar for both treatments and balance periods. These results support those of Noblet et al. (1983).

Energy and nitrogen output in milk from all sows increased during period 2 at a time when milk production would be expected to be maximal. Daily milk energy losses were the same for both groups, but milk yield was significantly lower ($P<0.01$) for the restricted-fed sows (6 $kg.d^{-1}$ versus 8 $kg.d^{-1}$ for high-fed sows). Sows on the restricted feeding level received 50% of the feed given to sows fed to appetite. Restricted-fed sows used both protein and fat from tissue reserves to meet the demand for milk production. These results agree with reports by others in which undernourished sows excreted less energy in their milk (de Lange et al., 1980; Noblet et al., 1983; Verstegen et al., 1985).

It is apparent that feed consumption is a primary determinant of the amount of body-tissue catabolism that occurs in support of milk production. Literature reviews by Aherne and Kirkwood (1985) and de Lange et al. (1980) suggest that voluntary feed consumption and weight change during lactation are influenced by level of feeding and weight gain during gestation. High gestation gains are associated with increased losses in the subsequent lactation. There is considerable evidence suggesting that body condition of sows at parturition influences efficiency of energy and nitrogen utilization during lactation (Libal and Wahlstrom, 1977; de Lange et al., 1980; Shields et al., 1985). Recent data suggest that protein intake during gestation and lactation plays an important role in post partum tissue catabolism and body weight change (Shields et al., 1985). Thus the effect of nutrition on sow metabolism may depend on the degree of dietary restriction imposed and on the physiological state at which it occurs. Our results support these conclusions.

Table II.1 Formulation and composition of the diet.

	% of diet
Ingredients	
Wheat	22.0
Barley	56.5
Soybean meal, 44% CP	14.5
Calcium phosphate	1.5
Limestone	1.0
Vitamin mineral premix†	1.0
Iodized salt	0.5
Tallow	3.0
Chemical analyses	
Dry matter, %	88.0
Crude protein, %	16.1
Lysine, %	0.74
Gross energy, $MJ.kg^{-1}$	16.5

†Supplied the following per kg of diet: 120 mg zinc, 12 mg manganese, 150 mg iron, 12 mg copper, 0.1 mg selenium, 5000 IU vitamin A, 500 IU vitamin D_3, 22 IU vitamin E, 12 mg riboflavin, 45 mg niacin, 24 mg calcium pantothenate, 500 mg choline, 30 μg vitamin B_{12}, 200 μg biotin. The diet for the restricted-fed sows was formulated to contain 2% vitamin-mineral premix.

Table II.2. Average daily feed intake (kg) during lactation of fed-to-appetite (high) and restricted-fed (low) sows.

Period	1				2		3	
Treatment	High		Low		High	Low	High	Low
	Gilts	Sows	Gilts	Sows	Sows	Sows	Sows	Sows
No. of observations	25	23	24	24	22	21	10	12
Week								
1	3.7	4.4	2.2	2.4	4.2	2.4	4.5	2.4
2	5.1	5.7	3.1	3.3	5.7	3.3	6.1	3.2
3	5.6	5.8	3.4	3.6	6.1	3.5	6.5	3.3
4	5.9	6.0	3.3	3.3	6.0	3.5	6.8	3.3
Mean	5.1 ± .24†	5.5 ± .21	3.0 ± .19	3.2 ± .34	5.5 ± .27	3.2 ± .26	6.0 ± .19	3.0 ± .25

†Values are means of weeks one through four plus or minus standard errors.

Table II.3. Effects of energy and protein restriction during lactation on sow liveweight change (kg) over three successive parities.

Period	1					2			3		
Treatment	High		Low			High	Low		High	Low	
	Gilts	Sows	Gilts	Sows	Sig.	Sows	Sows	Sig.	Sows	Sows	Sig.
No. of observations	25	23	24	24	NS	22	21	NS	10	12	NS
Breeding to Parturition Weight Change	56	45	54	44	NS	29	32	NS	8	12	NS
Lactation Weight Change											
Day 1 to Day 14	-7	-4	-16	-20	***	-3	-18	***	-1	-16	***
Day 14 to Day 28	23	-6	-10	-15	***	-8	-14	***	-2	-10	***
Breeding to Weaning Weight Change	66	36	28	8	***	18	2	***	5	-8	***

***P<0.001.

Table II.4. Effects of energy and protein restriction during lactation on sow backfat thickness (mm) for period 1.

Treatment	High		Low		Sig.
	Gilts	Sows	Gilts	Sows	
No. of observations	9	16	10	19	
Initial backfat thickness	21.4†	19.1	21.7	19.2	NS
Lactation Backfat Change					
Day 1 to Day 14	-1.0	-0.6	-4.6	-2.4	**
Day 14 to Day 28	-0.6	-0.4	-2.1	-3.6	**
Total Loss	-1.6	-1.0	-6.7	-6.0	**

†Gilts vs. sows ($P<0.05$) for both treatments.
**$P<0.001$.

Table II.5. Effect of feed intake during lactation on plasma levels of free fatty acids, urea nitrogen, glucose and creatinine for period 1.

	Day 2		Day 28		
Treatment	Low	High	Low	High	Sig.
Item					
Free fatty acids, mM^{-1}	0.29 ± .05†	0.25 ± .04	0.33 ± .03	0.25 ± .04	NS
Urea nitrogen, $mg.dL^{-1}$	29.7 ± 2.0	33.6 ± 2.7	37.9 ± 2.5	39.6 ± 2.4	NS
Glucose, $mg.dL^{-1}$	111.7 ± .06	101.9 ± .07	92.4 ± .05	94.8 ± .21	NS
Creatinine, $mg.dL^{-1}$	2.44 ± .24	2.36 ± .30	2.76 ± .14	2.11 ± .04	**

†Values are means plus or minus standard errors.
**$P<0.01$.

Table II.6. Effect of feed intake during lactation on energy and nitrogen balance of sows for period 1.

Balance Trial	I (Day 2-4)			II (Day 25-27)		
Treatment	High	Low	Sig.	High	Low	Sig.
No. of observations	4	5		4	5	
Energy, $MJ.d^{-1}$						
Intake	60 ± 11.42†	33 ± 4.70	*	78 ± 3.65	50 ± 4.90	***
Fecal	11 ± 2.02	6 ± 1.55	NS	17 ± 1.00	9 ± 0.70	***
Urine	3 ± 0.22	2 ± 0.31	NS	2 ± 0.29	2 ± 0.46	NS
Milk	22 ± 2.11	22 ± 1.23	NS	31 ± 1.28	28 ± 1.67	NS
Digestible energy, %	80 ± 4.06	85 ± 4.14	NS	78 ± 0.46	80 ± 2.00	NS
Metabolizable energy, %	75 ± 4.90	79 ± 2.63	NS	76 ± 0.54	76 ± 2.21	NS
Nitrogen, $g.d^{-1}$						
Intake	105 ± 15.47	54 ± 6.43	**	141 ± 6.91	81 ± 6.39	***
Fecal	15 ± 4.00	7 ± 2.01	NS	26 ± 1.38	13 ± 1.09	***
Urine	22 ± 4.86	13 ± 4.32	NS	20 ± 3.95	11 ± 3.16	NS
Milk	36 ± 2.98	39 ± 2.39	NS	59 ± 6.24	50 ± 5.30	NS
Balance	32 ± 7.13	-5 ± 5.04	***	36 ± 7.24	7 ± 3.04	**
Digestible nitrogen, %	86 ± 2.73	88 ± 3.37	NS	82 ± 1.05	84 ± 1.66	NS
Net nitrogen Utilization, %	57 ± 7.70	62 ± 6.39	NS	68 ± 1.86	71 ± 1.98	NS

†Values are means plus or minus standard errors.
*P<0.05, **P<0.01, ***P<0.001.

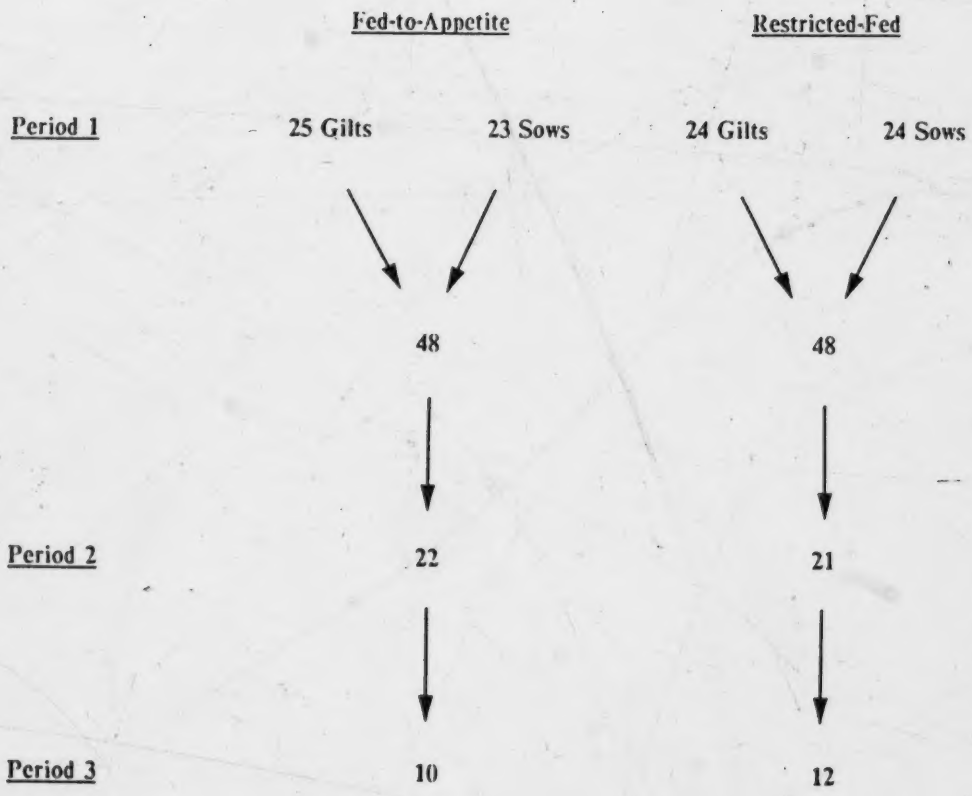

Figure II.1 Flow diagram illustrating the number of sows employed for each of the three lactation periods.

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III. MILK YIELD AND COMPOSITION, AND SOW REPRODUCTIVE PERFORMANCE

A. INTRODUCTION

For many years a great deal of interest has been focused on the relationship between energy (Reese et al., 1984; Noblet and Etienne, 1987), protein (Shields et al., 1985) or total nutrient (King and Dunkin, 1986a,b) intake during lactation and body condition of sows, and the effect of these parameters on sow and litter performance. Investigators have shown that excessive weight and/or fat loss during lactation adversely affects sow performance. Reports by Shields et al. (1985) and Verstegen et al. (1985) suggest that yield and composition of sows' milk depend upon body condition and nutrient intake. However, the amount of weight and/or fat a sow may lose before it affects her milk yield and composition, or delays return to estrus after weaning is not known. Futhermore the relative importance of dietary energy intake or the nutrient composition of the diet on the physiological and hormonal changes responsible for the observed poor reproductive performance is not clearly defined.

The objectives of this experiment were to study the consequences of chronic energy and protein restrictions on (1) milk yield and composition, (2) litter growth rate, and (3) sow reproductive performance.

B. MATERIALS AND METHODS

Experimental Design

The study was conducted with 49 primiparous and 47 multiparous (2nd to 5th parity) cross-bred sows. The sows were randomly assigned to groups that were fed to appetite (high) or fed a restricted (low) level during lactation. Twenty-two high-fed, and 21 restricted-fed sows were on trial for two consecutive parities (periods 1 and 2), and of these, 10 high and 12 restricted remained on test for a third parity (period 3). Some of the sows were assigned to a second experiment to determine the effects of exogenous gonadotrophin-releasing hormone on sow reproductive performance (Kirkwood et al., 1987) and therefore the numbers of sows in

each period decreased. From weaning to estrus, and during gestation the sows were housed in individual stalls within close proximity to a boar and fed 2.25 $kg.d^{-1}$ of a 16% crude protein diet which supplied 13.5 $MJ.kg^{-1}$ of digestible energy. On day 109 of gestation sows were weighed, and moved to raised farrowing crates in the farrowing unit. The temperature of the farrowing unit was maintained at 20°C. After farrowing the sows were fed a 16% crude protein diet during lactation (Table III.1) to a scale which allowed 10 (week 1), 13 (week 2), and 14 (weeks 3 and 4) percent of metabolic body weight ($kg^{0.75}$) for sows fed to appetite or 5 (week 1), 6.5 (week 2), and 7 (weeks 3 and 4) percent of metabolic body weight for restricted sows.

These lactation feed intake levels were derived in a preliminary study in which 11 multiparous cross-bred sows were fed a similar diet to appetite over a 28 day lactation. Average weekly feed intake was calculated as a percent of post-farrowing (day 1 of lactation) metabolic body weight.

The diet for restricted-fed sows was formulated with twice the amount of vitamin-mineral premix so that only protein and energy intake of those sows was restricted. Feed regimens were initiated the day after farrowing (day 1), and feed intake was measured daily throughout the 28 day lactation. Litter size was standardized to 8 pigs by day 3 of lactation and maintained at that number by substitution from litters of the same age whenever necessary. The pigs did not have access to creep feed. Pigs were weighed at birth and at weekly intervals throughout lactation.

Sows were weighed at breeding, day 109 of gestation, and on day 1, 14, and 28 of lactation. For nine fed to appetite and 12 restricted-fed sows, subcutaneous backfat samples were taken on day 2 and 28 of lactation. Adipose tissue samples were obtained using a variable-speed drill with an attached coring-cylinder from immediately behind the last rib and 4 cm lateral to the dorsal midline (Newell and Bowland, 1972). For biopsy, the area was shaved, and the skin was disinfected with surgical soap (Betadine scrub). A subcutaneous injection (2 mL) of local anesthetic (2% Lidocaine) was given. Following sampling the wound was treated with antiseptic powder. Tissue samples were immediately placed in plastic vials,

frozen, and stored at -23°C.

Milk production was estimated using a conversion of 4.0 g of milk per 1.0 g of pig gain (Lucas and Lodge, 1961). Milk ejection was accomplished by intramuscular injection of 1 mL of oxytocin (20 USP units per mL, Kovet Ltd.). Milk samples were obtained by hand-milking a thoracic, abdominal, and inguinal pair of teats on the 2nd and 28th day postpartum. The samples were stored at -20°C until needed for analysis.

Following weaning, sows were moved to gestation stalls within close proximity of a boar and were fed 2.25 $kg.d^{-1}$ of a 16% crude protein diet. A boar was used daily for detection of estrus and sows were mated on the first and second day of estrus. Sows in which estrus was not detected by day 25 postweaning were slaughtered and the reproductive tracts examined for signs of ovulation. Bred sows were slaughtered 25 days post coitum after being on trial for one or three consecutive lactation periods. Total number of corpora lutea present, number of normal, viable embryos, and number of abnormal embryos were recorded. Corpora lutea present on the ovaries were assumed to represent the number of ovulations. Data recorded at parturition included total number of pigs born, birth weight, and number and weights of pigs at weaning.

Laboratory Analyses

Milk samples were analyzed for protein (N x 6.38), fat, and lactose using an infra-red auto-milk analyzer (Milko Scan104, Foss Electric). Prior to analysis samples were thawed and homogenized using a polytron (Kinematica GmbH). Dry matter was determined following the AOAC 1980 procedure. The gross energy content of milk in calories per 100 g was calculated using the following formula:

$$E=9.11F + 5.12(6.38 \times TN) + 3.95L$$

where F, TN, and L are percentages of fat, total nitrogen, and lactose, respectively. The numerical values, 9.11, 5.12, and 3.95 are combustion factors in calories per gram of fat, protein and lactose, respectively (Perrin, 1954).

Extraction of milkfat from the milk was accomplished using a 50/50 (v/v) mixture of diethylether and petroleum ether. Adipose tissue samples were analyzed for individual fatty acids. Prior to lipid extraction (Folch et al., 1957), the outer layer of backfat was separated from the inner layer at the visible connective-tissue septum. The skin was removed from the outer layer of backfat and discarded. Methyl esters of the fatty acids were prepared as outlined by Morrison and Smith (1964). Methyl esters of individual fatty acids were separated by gas chromatography with an auto-injection chomatograph (Varian model 3700) and flame ionization detector. Methyl esters were partioned by a Quadrex glass capillary column (60 m x 0.25 mm I.D.) coated with Silar 10C. Separation was accomplished by temperature programming (6°C per min up to 198°C) with an initial column temperature of 100°C for 6 minutes. Temperature of the injection port was 250°C and the injection port was equipped with a splitter (100:1 split ratio). The flame ionization detector was maintained at 250°C. Nitrogen flow rate was 0.8 $mL.min^{-1}$. Fatty acids were identified by the use of reference standards (Supelco). A Hewlett Packard 3353 Data System was used to quantify the fatty acids by measuring peak areas, and they were expressed as percentages of the total fatty acids detected.

Statistical Analyses

Unless specified, the data were analyzed using MANOVA of SPSSX (SPSS Inc., 1983). Pregnancy rate and percent mortality were tested using the Fisher Exact Test, and fatty acid and milk composition were analyzed using the repeated measures design from the ANOVAR procedure of SPSSX (SPSS Inc., 1983).

C. RESULTS AND DISCUSSION

Milk Yield

The estimated change in average daily milk production over three successive lactations is shown in Table III.2. Milk yield was estimated by using a conversion factor of 4.0 g milk

per 1.0 g of pig gain. This value is the average conversion factor derived from the results of seven experiments (Lucas and Lodge, 1961) and is lower than the more recent value of 4.5 g of milk per 1.0 g of pig gain suggested by Lewis et al. (1978). It should be emphasized that many factors, both genetic and environmental, contribute to pig gain, and therefore milk yield calculated on the basis of suckling pig weight gain is subject to inaccuracy. Despite its limitations, this method of estimation serves to show relative differences in milk yield. Daily milk yield for all sows ranged from 4.4 to 7.6 $kg.d^{-1}$. This range in milk yield is similar to previous estimates of 5.0 to 8.0 $kg.d^{-1}$ reported by Lewis et al. (1978).

Feed consumption during lactation had a highly significant($P<0.01$) effect on milk yield. Sows fed to appetite produced an average of 7.5 kg of milk per day in each of the three lactation periods. In contrast, milk production for restricted-fed sows was 6.8, 5.8 and 4.4 $kg.d^{-1}$ for periods 1, 2 and 3, respectively. During period 1, restricted-fed sows produced as much milk per day as did the sows that were fed to appetite in spite of a lactation weight loss of 35 kg. However, in the subsequent lactations milk yield compared to sows fed to appetite was reduced by 1.7 and 3.1 $kg.d^{-1}$ for periods 2 and 3, respectively. It is apparent that these sows were unable to maintain milk production through the use of body reserves. The gestation feed intake of 2.25 $kg.d^{-1}$ was insufficient to replenish body stores to their original level and therefore consecutive lactations were begun with diminished body reserves from which to draw. These results are supported by those of Shields et al. (1985) and Verstegen et al. (1985) in which thin sows had significantly lower milk yields than sows in good body condition. It has been suggested by O'Grady et al. (1985) that lactating sows need to consume 6.5 $kg.d^{-1}$ (76.8 MJ $ME.d^{-1}$) in order to maintain body weight. This level is likely to be beyond the animals' appetite capacity and as a result most lactating sows experience loss of weight and mobilization of fat reserves (Reese et al., 1982a,b; King and Dunkin, 1986b; Noblet and Etienne, 1986) and muscle tissue (Reese et al., 1982a; Etienne et al., 1985) in order to maintain milk production.

Regardless of treatment, milk yield increased ($P<0.05$) with parity. Average milk yields per day were 6.7 kg for gilts, 7.1 kg for 2nd and 3rd parity sows, and 7.3 kg for sows

of four or more parities. Smith (1959) observed that milk yield increased from the first to the third lactation which is in agreement with the observations of Van Spaendonck (1967) over five successive lactations.

Milk Composition

Sows' milk contained approximately 17.7% dry matter, 4.7% protein, and 5.8% fat (Table III.3). These percentages are similar to those reported by Armstrong et al. (1986) but are slightly lower than those reported by Lucas and Lodge (1961). Results of den Hartog et al. (1986), suggest that milk composition is influenced by sampling method. Their studies showed that the dry matter, fat, lactose and energy contents of milk sampled after 2 mL (10 USP units mL^{-1} oxytocin injection were lower than was obtained after 1 mL oxytocin injection or by hand-milking. Similar to the results of Klaver et al. (1981), milk composition (period 1) was not greatly affected by feed level during lactation. Restriction of dietary energy (O'Grady et al., 1973) and protein (MacPherson et al., 1969) during lactation also failed to influence milk composition. The composition of milk from periods 2 and 3 was not determined and it is possible that it may have been affected by feed intake during these periods, when body reserves were markedly depleted.

Fatty Acid Composition

Fatty acid composition of sows' milk, and subcutaneous adipose tissue is shown Tables III.4 and III.5, respectively. Myristic, palmitic, palmitoleic, stearic, oleic, linoleic, and linolenic acids accounted for approximately 95% of the total fatty acids present in milk. These percentages are similar to literature values (Lodge et al., 1978; Reese et al., 1984). Regardless of feeding level, palmitic and oleic acids were the major milk fatty acids and comprised about 68% of the total fat. This agrees with results of Elliot et al. (1971), and Rastogi et al. (1980). Milk from restricted-fed sows had lower ($P<0.01$) amounts of 16-carbon fatty acids, while oleic and linoleic acids were present at higher ($P<0.01$) concentrations than in milk from sows fed to appetite. The quantity of stearic acid was greater while that of oleic acid was

lower in backfat of restricted-fed sows compared to backfat of sows fed to appetite. The percentage of oleic acid remained relatively constant over the lactation for high-fed sows but decreased ($P<0.05$) for restricted-fed sows. Milk and backfat obviously did not reflect dietary manipulations in the same way.

Reese et al. (1984) observed similar differences in subcutaneous adipose tissue from lactating sows fed varying levels of energy intake. It has been suggested that oleic is the most readily oxidized fatty acid in pigs (Seerley and Poole, 1974; Boyd et al., 1982) and this may account for the reduced oleic content of backfat from restricted-fed sows.

Sow and Litter Performance

The effects of energy and protein restriction during lactation on sow and litter performance are shown in Tables III.6 and III.7. Lactation feed level had no significant effect on pregnancy rate until period 3, at which time restricted-fed sows had significantly ($P<0.01$) lower pregnancy rates. Despite the lack of statistical significance large differences in pregnancy rate were observed. Sows fed to appetite had higher pregnancy rates than restricted-fed sows (91% versus 68% for period 1, and 91% versus 73% for period 2). At the time of breeding, the restricted-fed sows had completed three successive lactations on a nutritional regime which progressively depleted their body reserves. Previous reports by Elsley et al. (1969), Hitchcock et al. (1971), and Varley and Cole (1976) in which dietary energy and/or protein levels varied did not show an effect on pregnancy rate. The difference in results between these experiments may be due to variation in the body condition of the sows at the start of lactation and because their nutritional restriction was imposed over only one lactation.

Sows fed the restricted feeding level lost significantly ($P<0.01$) more weight than sows fed to appetite, but feeding level had no effect on ovulation rate, embryo number and embryo survival although large differences were observed. Several authors have reported that ovulation rate is not influenced by weight loss during lactation (King and Williams, 1984a,b; King and Dunkin, 1986c,d). Contrary to the results of the present study, King and Williams

(1984a,b) reported that low-level feeding adversely affected embryo survival. They did not detect differences in embryo survival of gilts fed varying levels of energy or protein during lactation.

For period 1 there was no significant difference in the incidence of anestrus between gilts (15%) and sows (20%) on the restricted feeding level. Fewer restricted-fed sows expressed estrus by day 25 postweaning than did sows fed to appetite ($P<0.01$). The incidence of anestrus for restricted-fed sows was 20, 25 and 22% for periods 1 through 3, respectively. All sows fed to appetite in periods 1 and 2, and 89% in period 3 exhibited estrus within 25 days postweaning.

Restricted-fed sows had significantly longer weaning to remating intervals than sows fed to appetite for periods 2 ($P<0.05$) and 3 ($P<0.01$). Extended weaning to remating intervals, and increased incidence of anestrus have been associated with extreme weight loss in lactation (King et al. 1982,1984; Reese et al., 1984; King and Williams, 1984a,b).

The number of pigs born was not affected by lactation feed level (Table III.7). Similar results have been reported by Reese et al. (1982) and Armstrong et al. (1986). However, the restricted-fed sows farrowed lighter weight ($P<0.05$) pigs in period 3. These sows entered gestation in poor body condition and it is likely that nutrients were being directed towards restoring body tissues, at the expense of fetal development, in preparation for lactation. Other studies (Elsley et al., 1969; O'Grady et al., 1973; Varley and Cole, 1976) failed to show an effect of nutrient restriction during lactation on birth weight. Again, this may be explained by the condition of the sows at the start of the nutritional regime, and by the relatively short experimental period which covered only one lactation.

Similarly, number of pigs weaned, percent mortality, and weaning weight were not influenced by low-level feeding until period 3. During this period, restricted-fed sows weaned fewer ($P<0.05$) pigs, and baby pig mortality was greater ($P<0.01$). Pigs weaned from restricted-fed sows averaged 6.0 kg in weight while those from sows fed to appetite averaged 7.6 kg during period 3. Low weaning weights of pigs from restricted-fed sows is probably due to the reduced milk yield. These results are similar to those of Reese et al. (1982) and Shields

et al. (1985). Experiments by Elsley et al. (1968), O'Grady et al. (1973), and Adam and Shearer (1975) failed to demonstrate differences in weaning weights of pigs from sows given high or low levels of dietary energy during lactation. However, these pigs had access to creep feed which may account for the differences observed.

During the third lactation, the average litter size weaned for restricted-fed sows was 6.4 pigs. The increase in mortality was most likely associated with a combination of factors including low birth weight (1.0 kg per pig versus 1.5 kg per pig for sows fed to appetite), reduced piglet vigor, impaired milk production, and increased sow agitation. The influence of nutrient intake on sow performance and ultimately litter performance, is most likely governed by the level of tissue reserves from which the sow has to draw; sows with adequate reserves being better able to withstand nutritional insult, and thus perform more normally, than sows in poor body condition.

Table III.1 Formulation and composition of the diet.

	% of diet
Ingredients	
Wheat	22.0
Barley	56.5
Soybean meal, 44% CP	14.5
Calcium phosphate	1.5
Limestone	1.0
Vitamin mineral premix†	1.0
Iodized salt	0.5
Tallow	3.0
Chemical analyses	
Dry matter, %	88.0
Crude protein, %	16.1
Lysine, %	0.74
Gross energy, $MJ.kg^{-1}$	16.5

†Supplied the following per kg of diet: 120 mg zinc, 12 mg manganese, 150 mg iron, 12 mg copper, 0.1 mg selenium, 5000 IU vitamin A, 500 IU vitamin D_3, 22 IU vitamin E, 12 mg riboflavin, 45 mg niacin, 24 mg calcium pantothenate, 500 mg choline, 30 μg vitamin B_{12}, 200 μg biotin. The diet for the restricted-fed sows was formulated to contain 2% vitamin-mineral premix.

Table III.2 Effect of energy and protein restriction during lactation on milk production ($kg.d^{-1}$).

Treatment	High		Low		
	Gilts	Sows	Gilts	Sows	Sig.
Period					
1	6.8†	7.5	6.6	6.8	**
2	—	7.5	—	5.8	**
3	—	7.6	—	4.4	**

†Gilts vs. sows ($P<0.05$) for animals fed-to-appetite.
**$P<0.01$.

Table III.3 Milk composition as percentage in fresh milk from sows fed-to-appetite vs. restricted-fed sows during lactation for period 1.

Treatment	High		Low		
Days of Lactation	2	28	2	28	SEM
No. of observations	12	12	12	12	
Component, %					
Dry matter	18.1	17.4	17.6	17.6	0.09
Protein	5.1	4.5	4.7	4.6	0.16
Fat	6.4	5.7	5.5	5.7	0.29
Lactose	5.4	6.0	5.8	5.8	0.11

Table III.4 Effect of protein and energy restriction during lactation (day 28) on fatty acid composition of sow's milk fat.

Treatment	High	SEM	Low	SEM	Sig.
No. of observations	12		12		
Fatty acid†					
14:0	3.5	0.16	3.1	0.16	
16:0	30.7	1.16	27.6	1.04	*
16:1	10.2	0.76	7.7	0.56	
18:0	4.5	0.17	4.6	0.22	
18:1	35.4	1.28	39.6	1.41	**
18:2	8.7	0.28	9.7	0.15	
18:3	2.4	0.02	2.5	0.02	

†Composition expressed as percentage of methyl esters.
*$P<0.05$, **$P<0.01$.

Table III.5. Effect of protein and energy restriction during lactation on the fatty acid composition of sow subcutaneous adipose tissue.

Days of Lactation	2				28			
Feed Intake	High	Low	SEM	Sig.	High	Low	SEM	Sig.
No. of observations	9	12			9	12		
Fatty acid†								
14:0	1.3	1.3	0.04	NS	1.2	1.2	0.5	NS
16:0	21.9	21.7	0.41	NS	21.9	22.4	0.56	NS
16:1	3.6	3.6	0.13	NS	3.4	3.4	0.11	NS
18:0	10.1	10.5	0.40	NS	10.7	11.6	0.61	*
18:1	49.3	49.3	0.75	NS	48.8	47.2	1.13	*
18:2	9.4	9.2	0.28	NS	9.6	9.4	0.30	NS
18:3	0.6	0.6	0.07	NS	0.7	0.6	0.09	NS

†Composition expressed as percentage of methyl esters.
*$P<0.05$.

Table III.6. The effects of energy and protein restriction during lactation on sow performance.

Period	1					2			3		
Treatment	High		Low			High	Low		High	Low	
	Gilts	Sows	Gilts	Sows	Sig.	Sows	Sows	Sig.	Sows	Sows	Sig.
No. of observations	25	23	24	24	NS	22	21	NS	10	12	NS
Pregnancy rate, %	94.1	91.2	68.4	68.4	NS	91.2	73.5	NS	83.3	42.8	**
Sows wt. change during lactation, kg	16	-10	-26	-35	**	-11	-37	**	-3	-26	**
Ovulation rate, no.	15.5	22.0	17.0	17.5	NS	19.9	19.4	NS	23.4	23.5	NS
Embryo no.	12.0	15.4	12.0	13.0	NS	19.9	14.2	NS	20.8	15.5	NS
Embryo survival, %	77.4	70.0	70.6	74.3	NS	87.3	72.1	NS	88.8	66.0	NS
Percent in estrus within 7 d postweaning	100	100	83	79	**	100	75	**	89	75	**
Incidence of anestrus, %	0	0	15	20	**	0	25	**	11	22	**
Remating interval, days	4.7	4.4	4.8	4.6	NS	4.4	5.2	*	4.0	6.1	**

*P<0.05, **P<0.01.

Table III.7. The effects of energy and protein restriction during lactation on litter performance.

Period	1				2		3		
Treatment	High		Low		High	Low	High	Low	
	Gilts	Sows	Gilts	Sows	Sows	Sows	Sows	Sows	Sig.
No. of observations	25	23	24	24	22	21	10	12	NS
Total born, no.	11.4	11.6	10.0	11.0	10.5	11.0	10.4	10.5	NS
Average birth wt., kg	1.3	1.4	1.3	1.4	1.4	1.4	1.5	1.0	*
No. weaned	7.8	7.9	8.0	8.0	8.0	7.8	7.7	6.4	*
Mortality	2.3	1.8	0.0	0.0	0.6	1.9	1.2	10.3	**
Average weaning wt., kg	7.6	8.2	7.0	7.5	8.0	6.8	7.6	6.0	NS

*$P<0.05$, **$P<0.01$.

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IV. PLASMA PROFILES OF CORTISOL, PROLACTIN, GROWTH HORMONE AND INSULIN ON DAYS 2 AND 28 OF LACTATION

A. INTRODUCTION

Postweaning anestrus in sows is an area currently receiving considerable attention. Numerous research articles have testified to the importance of the sow's energy status in the regulation of estrus (Reese et al., 1982, 1984; King and Williams, 1984a,b; Armstrong et al., 1986). However, few have attempted to identify the endocrine factors linking the body's energy-regulating components to subsequent reproductive performance. Consequently, there is a paucity of information about how hormones, other than the gonadotrophins, affect follicular development and the attainment of ovulatory estrus. Despite the lack of information, it is becoming increasingly evident that metabolic hormones and substrates play a role in linking the body's energy regulating components and the reproductive state of the animal. The present experiment aimed to study changes among a series of metabolically interrelated hormones, involved with the initiation and maintenance of lactation as well as with protein and amino acid metabolism, and lipolysis, and how these hormones may influence the post weaning secretion of reproductive hormones.

The objective of this study was to determine the effects of feed restriction during lactation on 24 hour plasma profiles of cortisol, prolactin, growth hormone and insulin on day 2 and 28.

B. MATERIALS AND METHODS

Experimental Design

The study was conducted with 49 primiparous and 47 multiparous (2nd to 5th parity) cross-bred sows. The sows were randomly assigned to groups that were fed to appetite (high) or fed at a restricted (low) level during lactation. From weaning to estrus, and during gestation the sows were housed in individual stalls within close proximity to a boar and fed

2.25 $kg.d^{-1}$ of a 16% crude protein diet which supplied 13.5 $MJ.kg^{-1}$ of digestible energy. One day 109 of gestation sows were weighed, and moved to raised farrowing crates in the farrowing unit. The temperature of the farrowing unit was maintained at 20°C. After farrowing the sows were fed a 16% crude protein diet during lactation (Table IV.1) to a scale which allowed 10 (week 1), 13 (week 2), and 14 (weeks 3 and 4) percent of metabolic body weight ($kg^{0.75}$) for sows fed to appetite or 5 (week 1), 6.5 (week 2), and 7 (week 3 and 4) percent of metabolic body weight for restricted sows.

These lactation feed intake levels were derived in a preliminary study in which 11 multiparous cross-bred sows were fed a similar diet to appetite over a 28-day lactation. Average weekly feed intake was calculated as a percent of post-farrowing (day 1 of lactation) metabolic body weight.

The diet for restricted-fed sows was formulated with twice the amount of vitamin-mineral premix so that only protein and energy intake of those sows was restricted. Feed regimens were initiated the day after farrowing (day 1), and feed intake was measured daily throughout the 28 day lactation. Litter size was standardized to 8 pigs by day 3 of lactation and maintained at that number by substitution from litters of the same age whenever necessary. The pigs did not have access to creep feed. Pigs were weighed at birth and at weekly intervals throughout lactation. Blood samples (10 to 15 mL) were collected hourly over a 24-hour period from 8 high-fed and 7 restricted-fed sows on days 2 and 28 of lactation (period 1). The blood samples were obtained from ear vein cannulas (Evans, 1987) and collected into heparinized glass tubes. The samples were placed on ice and centrifuged within 24 hours of collection. The plasma from each sample was divided into 3 aliquots and transferred to sterile plastic vials (1.25 x 2.5 cm) and stored at -20°C until required for analysis. The samples were used for one freeze-thaw cycle only.

Hormone Assays

Cortisol

All plasma samples (5 μL per tube) were assayed for cortisol concentration by the method of Evans et al. (1987), using rabbit anticortisol-3-oxime-BSA (Endocrine Sciences, USA). Accuracy, evaluated by adding known quantities of standard (Hydrocortisone, Sigma) to control plasma and determining recovery was 96.3 ± 1.3%, intra- and inter-assay CV were 3.5 and 8.2 respectively, and assay sensitivity was 0.2 ng per tube. The inhibition curve for cortisol generated by plasma volumes ranging from 1 to 50 μL was parallel to the standard curve.

Prolactin

Plasma prolactin (PRL) concentration was determined by the method of Mulloy and Malven (1979). Purified porcine PRL (LER-2073) was used as the radioiodinated antigen and standard, and anti-porcine PRL (ALM-5) as the antisera. All samples (20 μL) were analyzed in duplicate within the same assay. Sensitivity of the assay was 0.2 ng per assay tube. For recovery estimation, five quantities of standard pPRL (1 to 8 ng) were added to 50 μL of control plasma. Recovery was estimated at 98.2 ± 2.3%. The inhibition curve generated from increasing amounts of plasma (2 to 50 μL) was parallel to the standard curve. Intra-assay CV was 7.5%.

Growth Hormone

Plasma growth hormone (GH) concentration was determined by the method of Marple and Aberle (1972) as validated in this laboratory by Kirkwood et al. (1987). All samples were processed in a single assay in which the intra-assay CV and sensitivity were 7.0% and 0.4 ng per assay tube, respectively.

Insulin

Insulin (INS) determinations were made by the method of Ray et al. (1983). Purified porcine INS (Calbiochem) was used as the radioiodinated antigen and standard, and INS antiserum IN-40 (Endocrine Sciences) as the antisera. All samples (50 μL) were analyzed in duplicate within the same assay. Sensitivity of the assay was 1 μU per assay

tube. For recovery estimation, five quantities of porcine INS (1 to 5 μU) were added to 50 μL of control plasma. Recovery was estimated at 95.3 $\pm$ 2.1%. The inhibition curve generated from increasing amounts of plasma (10 to 100 μL) was parallel to the standard curve. Intra-assay CV was 5.1%.

Statistical Analyses

Significant elevations of the plasma hormones were determined by the method of Veldhuis et al. (1985). Individual plasma concentrations were considered as peaks if their value exceeded four times their intra-assay coefficients of variation from the preceding nadir. Baseline was calculated as the average of all non-peak and nadir points. Data were analyzed by Student's t-test (Steel and Torrie, 1980).

C. RESULTS AND DISCUSSION

Cortisol

Plasma cortisol concentrations were greater ($P<0.05$) in restricted sows than in fed-to-appetite sows on both days 2 and 28 of lactation (Table IV.2). The elevated cortisol level in restricted-fed sows was most likely the result of a slightly greater baseline and average peak magnitude (Table IV.3). Elevated plasma cortisol levels have also been observed in underfed macque-monkeys (Steiner, 1987) and malnourished humans (Alleyne and Young, 1967; Lunn et al., 1973).

Corticosteroids are known to have profound effects on intermediary metabolism, particularly in fasting animals (Bentley, 1982). Cortisol increases gluconeogenesis in the liver, and inhibits the uptake and incorporation of amino acids into muscle protein. Cortisol is also known to enhance the lipolytic effects of epinephrine and GH (Bentley, 1982). An excess of cortisol promotes muscle wasting and a negative nitrogen balance (Bentley, 1982). The increased levels of circulating cortisol on day 28 are possibly associated with greater body tissue catabolism in the present study, since the plasma concentrations of free fatty acids and creatinine were higher in restricted-fed sows at this

time (0.33 versus 0.25 mM for free fatty acids, and 2.76 versus 2.11 $mg.dL^{-1}$ for creatinine, for restricted-fed and fed-to-appetite sows, respectively). There was a linear relationship ($r=.45$, $P<0.01$) between 28 day plasma cortisol level and weight loss, providing further support for the suggested catabolic effect of cortisol.

Excessive weight and/or fat loss during lactation adversely affects sow reproductive performance (King and Dunkin, 1986a,b; Noblet and Etienne, 1986), which is thought to be the result of reduced gonadotrophin secretion. In the present experiment the incidence of anestrus was 20 percent for restricted-fed sows, while all sows fed-to-appetite exhibited estrus within 25 days postweaning. Possibly the elevated levels of plasma cortisol influenced the occurrence of anestrus. Some evidence implicating the role of cortisol in the incidence of anestrus is found in the work of Kunavongkrit (1984, cited by Britt et al., 1985) which looked at plasma cortisol levels in zero-weaned sows and sows nursing small (2 to 6 pigs) or normal (7 to 9 pigs) litters. Anovulatory zero-weaned sows had elevated plasma levels of cortisol during the first two weeks after parturition relative to those sows that ovulated within two weeks post partum. Cortisol concentrations in sows nursing small and normal size litters were similar to those observed in the anovulatory zero-weaned sows. It is possible that the elevated cortisol levels block the ability of estradiol to induce the positive feedback surge of LH.

Prolactin (PRL)

No treatment effect was noted for mean plasma PRL concentrations at either stage of lactation (Table IV.2). Prolactin levels for day 28 were similar to those previously reported (Kirkwood et al., 1984). The PRL values determined on day 2 (43.7 $\pm$ 5.4 ng mL^{-1}, 49.6 $\pm$ 6.0 mg mL^{-1} for restricted-fed and fed-to-appetite, respectively) differ from those of Bevers et al. (1978) and Mulloy and Malven (1979) who found lower plasma PRL concentrations in sows during early lactation (8 to 30 ng mL^{-1}, 27 $\pm$ 5 ng mL^{-1}, respectively). These differences are due to different sampling intervals and to piglet access to the sows.

The number of PRL peaks occurring on day 28 was different ($P<0.05$) between the treatment groups (Table IV.3). Six of the fed-to-appetite sows maintained a constant secretion pattern compared to the restricted-fed sows in which 5 of 7 had at least one significant elevation. Milk production in restricted-fed sows was markedly depressed ($P<0.01$, Chapter II) and since the pigs from these sows were receiving less milk they may have been more aggressive in their nursing and so influenced PRL secretory patterns.

Regardless of treatment, PRL concentration decreased as the lactation progressed, which concurs with the data of Bevers et al. (1978), van Landeghem and van de Wiel (1978), and Mulloy and Malven (1979). This consistent finding has been explained on the basis of changing milk yield (Mulloy and Malven, 1979) and/or suckling intensity (van Landeghem and van de Wiel, 1978; Armstrong et al., 1986). In agreement with the findings of Bevers et al. (1978), no clear diurnal rhythm for plasma PRL was found in this study.

Growth Hormone (GH) and Insulin (INS)

In the present experiment no differences were apparent in plasma GH or INS on day 2 of lactation (Table IV.2). Feed restriction resulted in elevated plasma GH ($P<0.01$) and depressed INS ($P<0.01$) on day 28 of lactation. As shown in Table IV.4, restricted-fed sows had a greater basal level ($P<0.05$), peak frequency ($P<0.05$) and average peak magnitude ($P<0.01$) of plasma GH. In these sows, fewer significant elevations of plasma INS were noted ($P<0.01$).

Growth hormone is a potent adipokinetic agent that functions in an antagonistic way to INS (Machlin et al., 1968). The modified levels of GH and INS seen in restricted-fed sows probably reflected a physiological attempt at meeting the demands of lactation by partitioning nutrients toward the mammary gland. Catabolism of body reserves may be the result of changes in the relative activities of both GH and INS; growth hormone causing mobilization of adipose stores, and lowered levels of INS reducing tissue synthesis. A highly significant, positive correlation between plasma GH concentration and weight loss was found ($r=.68$, $P<0.01$). Insulin concentration was

inversely related to weight loss ($r=-.44$, $P<0.05$).

In contrast to this study, Armstrong et al. (1986) failed to show an effect of restricted feeding on plasma levels of INS in lactating sows. In their experiment energy restriction had no effect on reproductive performance or reproductive hormones dispite the greater weight and backfat loss of restricted-fed sows relative to sows fed ad libitum. Possibly the effect of energy restriction on hormone concentration was masked by the greater protein intake of the restricted-fed sows compared to the sows fed ad libitum (630 vs. 568 $g.d^{-1}$ for restricted-fed vs. ad libitum-fed, respectively). Another factor that may have influenced the results obtained in Armstrong et al.'s study was the limited blood sampling. Insulin concentrations were determined on the basis of a single sample taken on days 6, 12 and 20 of lactation and as a result true differences may have been missed.

An attractive hypothesis which suggests a role for INS in reproductive processes has been proposed by Steiner (1987). This author has suggested that INS may provide a link between nutritional status and reproductive function. Insulin binds to receptors in the arcuate nucleus and the median eminence thus influences the availability of substances essential for the synthesis of norepinephrine and serotonin (Fernstrom, 1983), both of which are thought to function in the control of GnRH secretion (Steiner, 1987).

In summary, the mechanism by which nutritional status alters reproductive function remains speculative. However, these results suggest that cortisol and INS may in part be responsible.

Table IV.1 Formulation and composition of the diet.

	% of diet
Ingredients	
Wheat	22.0
Barley	56.5
Soybean meal, 44% CP	14.5
Calcium phosphate	1.5
Limestone	1.0
Vitamin mineral premix†	1.0
Iodized salt	0.5
Tallow	3.0
Chemical analyses	
Dry matter, %	88.0
Crude protein, %	16.1
Lysine, %	0.74
Gross energy, $MJ.kg^{-1}$	16.5

†Supplied the following per kg of diet: 120 mg zinc, 12 mg manganese, 150 mg iron, 12 mg copper, 0.1 mg selenium, 5000 IU vitamin A, 500 IU vitamin D_3, 22 IU vitamin E, 12 mg riboflavin, 45 mg niacin, 24 mg calcium pantothenate, 500 mg choline, 30 μg vitamin B_{12}, 200 μg biotin. The diet for the restricted-fed sows was formulated to contain 2% vitamin-mineral premix.

Table IV.2 Average daily plasma concentrations of cortisol, prolactin, growth hormone and insulin in multiparous sows during lactation.

Treatment	Day of Lactation 2	28
	Cortisol, $ng.mL^{-1}$	
Fed-to-appetite†	10.0 ± 0.7‡	9.6 ± 0.7
Restricted-fed	12.8 ± 0.6	12.6 ± 0.9
Sig.	•	•
	Prolactin, $ng.mL^{-1}$	
Fed-to-appetite	49.6 ± 6.0	19.1 ± 0.6
Restricted-fed	43.7 ± 5.4	18.2 ± 0.4
Sig.	NS	NS
	Growth hormone, $ng.mL^{-1}$	
Fed-to-appetite	3.1 ± 0.2	2.5 ± 0.1
Restricted-fed	3.1 ± 0.1	3.8 ± 0.2
Sig.	NS	••
	Insulin, $\mu U.mL^{-1}$	
Fed-to-appetite	17.3 ± 3.7	6.3 ± 0.6
Restricted-fed	9.1 ± 1.2	4.0 ± 0.3
Sig.	NS	••

†Values are means of 8 fed-to-appetite and 7 restricted-fed sows.
‡Values are means plus or minus standard errors.
•$P<0.05$, ••$P<0.01$.

Table IV.3. Plasma profiles of cortisol and prolactin in multiparous sows fed-to-appetite (high) or restricted-fed (low) during lactation.

Treatment	Day of lactation	Baseline, ng.mL^{-1}	Frequency of peak, no. per 24 h	Average peak magnitude, ng.mL^{-1}
			Cortisol	
High†	2	7.0 ± 1.4‡	7.2 ± 0.3	14.2 ± 1.0
Low	2	8.5 ± 0.5	7.8 ± 0.6	18.9 ± 2.4
Sig.		NS	NS	NS
High	28	6.8 ± 0.9	6.8 ± 0.5	14.4 ± 1.1
Low	28	9.7 ± 1.3	7.0 ± 0.4	17.7 ± 1.4
Sig.		NS	NS	NS
			Prolactin	
High	2	44.7 ± 5.1	4.0 ± 0.3	64.3 ± 9.0
Low	2	49.4 ± 8.6	2.5 ± 0.6	57.5 ± 12.2
Sig.		NS	NS	NS
High	28	18.8 ± 0.4	0.5 ± 0.3	37.8 ± 4.0
Low	28	17.7 ± 0.4	1.8 ± 0.4	22.2 ± 2.7
Sig.		NS	*	NS

†Values are means of 8 fed-to-appetite and 7 restricted-fed sows.
‡Values are means plus or minus standard errors.
*$P<0.05$.

Table IV.4. Plasma profiles of growth hormone and insulin in multiparous sows fed-to-appetite (high) or restricted-fed (low) during lactation.

Treatment	Day of lactation	Baseline, ng mL^{-1} or μU mL^{-1}	Frequency of peak, no. per 24 h	Average peak magnitude, ng mL^{-1} or μU mL^{-1}
		Growth hormone		
High†	2	3.0 ± 0.1‡	2.8 ± 0.8	3.7 ± 0.2
Low	2	2.7 ± 0.1	5.3 ± 0.6	4.2 ± 0.3
Sig.		NS	*	NS
High	28	2.2 ± 0.1	4.8 ± 0.4	3.6 ± 0.3
Low	28	3.4 ± 0.4	6.2 ± 0.4	5.4 ± 0.5
Sig.		*	*	**
		Insulin		
High	2	9.0 ± 2.1	5.9 ± 0.5	27.2 ± 5.6
Low	2	6.7 ± 0.7	5.5 ± 0.6	14.5 ± 1.4
Sig.		NS	NS	NS
High	28	3.3 ± 0.1	5.2 ± 0.2	13.1 ± 1.4
Low	28	3.0 ± 0.1	4.3 ± 0.7	7.2 ± 0.8
Sig.		NS	NS	**

†Values are means of 8 fed-to-appetite and 7 restricted-fed sows.
‡Values are means plus or minus standard errors.
*$P<0.05$, **$P<0.01$.

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V. GENERAL DISCUSSION

Man's interest in the effects of nutrition on reproduction has been aroused for nearly a century, and some of the factors in the regulation of reproduction in many mammalian species have been published. These publications have left us with detailed descriptions of the effects of malnourishment on reproductive disturbances and it remains unchallenged that variables such as body size, body fat, and metabolic rate are somehow associated with the reproductive axis. Despite our collective knowledge no mechanisms on how the body "knows" its size or levels of reserves have been explained.

Early swine research, in this field of study, has received criticism for being of insufficient duration. With this in mind the present experiment was conducted over three consecutive parities. The importance of this cannot be overestimated since the sow normally has sufficient body reserves to utilize over the short-term. Thus, experiments of short duration would not show the long-term effects of malnutrition and this may lead to errorneous conclusions. Of equal importance are the indirect effects of each stage of reproduction on the next stage. It is imperative that future research considers this, as it is becoming increasingly apparent that reproductive stages are not discrete and that nutrition for a particular stage has both direct and indirect effects on sow productivity.

The results of the present experiment indicate that excessive weight and fat loss is detrimental to sow productivity. Sows on the restricted feeding level lost significantly more weight and backfat than sows fed-to-appetite. Since the gestation feed level was insufficient to replenish body reserves to their original level in restricted-fed sows, each consecutive lactation was begun with diminished body reserves from which to draw. Depletion of body reserves was manifested by depressed milk yield, and consequently reduced piglet growth. It must be emphasized that the effects of restricted-feeding were not observed in period 1 which provides support for the recommendation that experiments of this nature must be of longer duration than one parity.

Restricted feeding had no significant effect on ovulation rate, embryo number or embryo survival but was associated with an increased incidence of anestrus, and extended

weaning to remating interval. There were no differences in the number of pigs born but piglet birth weight was significantly lower for restricted-fed sows in period 3.

Although body composition of the sows used in this experiment was not determined, there does appear to be an association between weight loss and body composition and alternations in reproductive performance. It has been suggested that an as yet unidentified minimum percentage of body fat is required for normal functioning of the reproductive system (Frish and McArthur, 1974; Kirkwood and Aherne, 1985). Some light has been shed on this problem by studying the effects of metabolic stresses on reproductive performance. For example, severe weight loss as the result of restricted energy intake is associated with depressed gonadotropin secretion resulting from inhibition of gonadotropin-releasing hormone (GnRH) secretion (Kirkwood et al., 1984; Armstrong and Britt, 1985). A similar reduction in gonadotropin secretion as the result of inhibited GnRH secretion in seen in adult women with severe weight loss caused by anorexia nervosa (Boyar et al., 1974). Nutritional therapy and weight gain in these women is associated with restored gonadotropin-releasing hormone and increased plasma levels of luteinizing hormone (LH) and follicle-stimulating hormone (Warren et al., 1980). Thus there is convincing evidence supporting the relationship between nutrition and the maintenance of normal reproductive function.

Reproductive function is influenced by other metabolic stressors, besides weight loss. Severe exercise resulting in low body fat reserves, such as in ballet dancers, is frequently associated with amenorrhea (Frisch et al., 1980). However, if their exercise program is interrupted, menstrual cycling may resume without a concurrent increase in body weight (Warren, 1980). These observations led Warren (1980) and Steiner (1987) to suggest that it is not body composition per se that results in alterations of reproductive function but rather some factor of metabolic status that reflects energy demands on the body, as well as body composition.

The present experiment was designed to study the effects of restricted feed intake on plasma levels of selected metabolic hormones, as a step toward identifying the metabolic factor(s) linking body metabolism with reproduction function. The results from this

experiment show that restricted feeding influenced plasma levels of cortisol, growth hormone (GH) and insulin (INS) but had little effect on prolactin.

Plasma cortisol concentrations were higher in restricted-fed sows than in sows fed-to-appetite on days 2 and 28 of lactation. This phenomenon of elevated plasma cortisol in association with underfeeding has also been observed in monkeys (Steiner, 1987) and in humans (Alleyne and Young, 1967; Lunn et al., 1973). Dubey and Plant (1985) were able to inhibit LH and FSH secretion in rhesus monkeys by administration of hydrocortisone acetate. These authors have suggested that the hydrocortisone acetate action is mediated at the level of the central nervous system. These data suggests that stress and the subsequent glucocorticoid secretion may play a role in suppressing GnRH under conditions of malnourishment.

The modified levels of GH and INS seen in restricted-fed sows are probably associated with a physiological attempt at meeting the demands of lactation by partitioning nutrients toward the mammary gland. Restricted-fed sows had higher plasma INS concentrations than sows fed-to-appetite. This effect of underfeeding on plasma INS levels has also been observed in monkeys (Steiner, 1987). An attractive hypothesis which suggests a role for INS in reproductive processes has been proposed by Steiner (1987). This author has suggested that INS may provide a link between nutritional status and reproductive function. Insulin acts on the brain and influences the availability of substances required for the synthesis of neurotransmitters involved with control of GnRH secretion (Steiner, 1987).

In conclusion, this experiment is another step toward our ultimate goal of identifying the elusive metabolic factors regulating body metabolism and reproductive performance. The results support a role for cortisol and insulin in suppression of GnRH, but clearly further experimentation is required. A better understanding of this problem would benefit, not only animal production, but has implications for human health as well.

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